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Climatic Influences on Human Body Size and Proportions: Ecological Adaptations and Secular Trends

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ABSTRACT This study reevaluates the long-standing observation that human morphology varies with climate. Data on body mass, the body mass index [BMI; mass (kg)/stature (m)^2], the surface area/body mass ratio, and relative sitting height (RSH; sitting height/stature) were obtained for 223 male samples and 195 female samples derived from studies published since D.F. Roberts' landmark paper "Body weight, race, and climate" in 1953 (Am. J. Phys. Anthropol. 11:533–558). Current analyses indicate that body mass varies inversely with mean annual temperature in males ($r = -0.27$, $P < 0.001$) and females ($r = -0.28$, $P < 0.001$), as does the BMI (males: $r = -0.22$, $P = 0.001$; females: $r = -0.30$, $P < 0.001$). The surface area/body mass ratio is positively correlated with temperature in both sexes (males: $r = 0.29$, $P < 0.001$; females: $r = 0.34$, $P < 0.001$), whereas the relationship between RSH and temperature is negative (males: $r = -0.37$, $P < 0.001$; females: $r = -0.46$, $P < 0.001$). These results are consistent with previous work showing that humans follow the ecological rules of Bergmann and Allen. However, the slope of the best-fit regressions between measures of body mass (i.e., mass, BMI, and surface area/mass) and temperature are more modest than those presented by Roberts. These differences appear to be attributable to secular trends in mass, particularly among tropical populations. Body mass and the BMI have increased over the last 40 years, whereas the surface area/body mass ratio has decreased. These findings indicate that, although climatic factors continue to be significant correlates of world-wide variation in human body size and morphology, differential changes in nutrition among tropical, developing world populations have moderated their influence. Am J Phys Anthropol 106:483–503, 1998.

Since the emergence of the genus *Homo* in tropical Africa, hominids have spread to virtually every ecosystem on earth. Thus, human populations have been exposed to a wide variety of different ecological stressors. Adaptation to these widely differing, selective pressures, explains, in part, why *H. sapiens* is such a diverse, polytypic species.

Thermal stress represents one of the most variable constraints to which humans have had to adapt. Variation in both physiological and morphological responses to temperature stress has been widely documented among both humans and nonhuman species. Two so-called ecological rules are often cited

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TABLE 1. Temporal distribution of the current samples[1]

Year of study	Males	Females
1953–1959	1	2
1960–1969	63	55
1970–1979	80	55
1980–1989	58	57
1990–1996	21	26
Total	223	195

[1] Number of samples used varies among variables. The reported numbers are for body mass.

TABLE 2. Geographic distribution of the current sample and Roberts' (1953) sample[1]

Region	Males	Females	Roberts (males)[2]
African	44	41	28
Australian	11	6	2
Melanesian	47	41	4
American	55	47	16
European	17	18	20
Central Asian	6	7	2
East Mongoloid	11	8	29
Polynesian	13	12	2
South Asian	4	1	6
Indian	15	14	7
Total	223	195	116

[1] Sample sizes vary among variables. The reported sample size is for body mass.
[2] Data from Roberts (1953).

when examining anthropometric variation and its association with climatic stress in mammals. The Bergmann rule states that, "within a polytypic warm-blooded species, the body size of the subspecies usually increases with decreasing mean temperature of it's habitat" (Bergmann, 1847). Allen's rule states that, "in warm-blooded species, the relative size of exposed portions of the body decreases with decrease of mean temperature" (Allen, 1877). It has long been suggested that the ecological rules may apply to humans (Ridgeway, 1908; Schreider, 1950, 1957, 1964, 1971, 1975; Roberts, 1953, 1973, 1978; Barnicot, 1959; Baker, 1966; Walter, 1971; Ruff, 1994).

In general, humans do appear to follow the ecological rules of Bergmann (1847) and Allen (1877), such that those individuals inhabiting colder regions are heavier and have shorter relative limb lengths, resulting in a decreased ratio of surface area to body mass. Schreider (1950) was among the first to demonstrate the association between body mass/surface area and geography among humans. However, the most widely cited work is Roberts' (1953) classic study, "Body weight, race, and climate." By using anthropometric data from 116 male samples and 33 female samples, Roberts demonstrated a significant negative correlation between body mass and mean annual temperature, indicating that humans appear to conform to Bergmann's rule. In a subsequent analysis of relative sitting height and mean annual temperature, Roberts (1973) demonstrated that humans also appear to conform to Allen's rule, such that populations living in colder regions have relatively shorter legs than those groups inhabiting hotter areas.

Several authors have since published regional studies related to climate and body size in Africa (Hiernaux, 1968; Hiernaux and Froment, 1976), Europe and the Mediterranean (Crognier, 1981), and the New World (Newman, 1953; Newman and Munro, 1955; Stinson, 1990). However, Roberts' statistical analyses have not been replicated on a worldwide scale. Roberts' subsequent versions (1973, 1978) are often cited, but, inevitably, all citations lead back to the original analysis of 116 male samples in 1953. In a recent review, Ruff (1994) presented an analysis of 56 modern human samples (males and females combined) in relation to latitude rather than mean annual temperature. The results indicated a significant positive relationship between body mass and absolute values of latitude; however, the freshness of the data was unclear, because the majority of the samples were taken from Eveleth and Tanner (1976).

The purpose of this study is to reevaluate the influence of climate on human body size and proportions by using anthropometric data published subsequent to Roberts' initial work (1953). Given the remarkable changes that have occurred in physical growth among human populations over the last 40 years, it is expected that the relationship between climate and body size documented by Roberts will have changed as well. These changes should help to provide insights into the roles of different environmental factors in shaping worldwide variation in human body size and morphology.

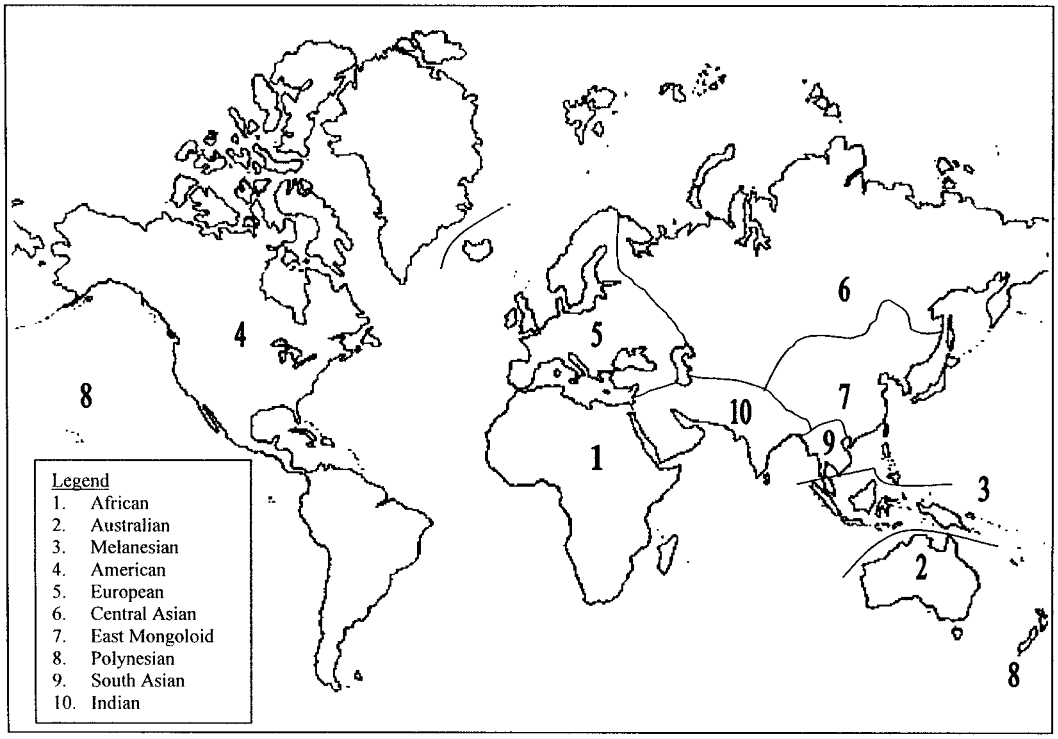

Fig. 1. Geographic grouping of the samples included in this study (groupings derived from Roberts, 1953).

MATERIALS AND METHODS

Sample

Data on mean stature (cm) and body mass (kg) were obtained for 223 male samples and 195 female samples from studies published on adults (age ≥18 years) since 1953. For a subsample of these studies (n = 165), data on sitting height were also available. The distribution of studies by year of publication is shown in Table 1. The studies range in age from to 1 year to 44 years from the current date, with the majority of the studies published since 1960. The samples were drawn largely from the physical anthropology literature, and the representativeness of the samples of the general populations from which they were drawn cannot be determined, because most studies relied on volunteers. In addition, the samples were not weighted for the size of the population that they represent.

The geographic distribution of the samples is outlined in Table 2 and in Figure 1. Mean annual temperatures for the geographic areas from which the anthropometric data were collected were obtained from climatic tables and atlases (Steinhauser, 1970; Schwerdtfeger, 1976; Gentilli, 1977; Lydolf, 1977; Steinhauser, 1979; Willmott et al., 1981).

TABLE 3. Regression parameters for the relationships between selected anthropometric dimensions (weight, BMI, SA/mass, and RSH) and mean annual temperature among Robert's (1953) sample and among men and women of the current sample[1]

Sample	n	Constant	b	SE	r	P
Roberts' males						
Body mass	116	65.80	−0.546	0.070	−0.589	<0.001
BMI	116	23.41	−0.141	0.018	−0.586	<0.001
SA/mass	116	2.68	0.012	0.001	0.594	<0.001
Males						
Body mass	223	66.86	−0.261	0.063	−0.267	<0.001
BMI	222	23.62	−0.058	0.017	−0.221	0.001
SA/mass	222	2.67	0.005	0.001	0.288	<0.001
RSH	94	52.97	−0.062	0.016	−0.369	<0.001
Females						
Body mass	154	59.36	−0.259	0.064	−0.279	<0.001
BMI	153	24.42	−0.088	0.020	−0.295	<0.001
SA/mass	153	2.74	0.006	0.001	0.341	<0.001
RSH	71	53.68	−0.066	0.016	−0.456	<0.001

[1] BMI, body mass index; SA, surface area; RSH, relative sitting height; SE, standard error.

TABLE 4. Multiple regression analyses evaluating the influence of mean annual temperature and "year of study publication" on selected measures of body size and proportion

			Temperature			Year				
Sample	n	Constant	b	SE	*P*	b	SE	*P*	R*	*P*
Males										
Body mass	223	−165.05	−0.266	0.063	<0.001	0.117	0.064	0.070	0.29	<0.001
BMI	222	−80.75	−0.060	0.017	<0.001	0.053	0.017	0.003	0.30	<0.001
SA/mass	222	6.91	0.005	0.001	<0.001	−0.002	0.001	0.056	0.31	<0.001
RSH	94	108.67	−0.058	0.016	0.001	−0.028	0.020	0.160	0.39	<0.001
Females										
Body mass	154	−208.98	−0.275	0.064	<0.001	0.136	0.063	0.032	0.32	<0.001
BMI	153	−82.42	−0.094	0.020	<0.001	0.054	0.020	0.007	0.35	<0.001
SA/mass	153	7.93	0.007	0.001	<0.001	−0.003	0.001	0.038	0.37	<0.001
RSH	71	110.90	−0.062	0.016	<0.001	−0.029	0.020	0.161	0.48	<0.001

* Coefficient of multiple determination. SE, standard error; BMI, body mass index; SA, surface area; RSH, relative sitting height.

TABLE 5. Differences in body mass, BMI, and SA/mass between males of Roberts (1953) and the current sample[1]

	Roberts (1953)			Current sample					
	n	M	SD	n	M	SD	Δ	t	*P*
Total									
Body mass	116	56.5	7.9	223	61.6	9.5	+5.1	4.92	<0.001
BMI	116	21.0	2.0	222	22.4	2.5	+1.4	5.21	<0.001
SA/mass	116	2.87	0.18	222	2.77	0.16	−0.10	5.46	<0.001
≤14.9°C									
Body mass	43	61.9	6.2	46	66.6	6.9	+4.7	3.37	0.001
BMI	43	22.4	1.6	46	23.4	1.7	+1.0	2.76	0.007
SA/mass	43	2.76	0.11	46	2.68	0.11	−0.08	3.33	0.001
≥15.0°C									
Body mass	73	53.4	7.0	177	60.3	9.6	+6.9	5.54	<0.001
BMI	73	20.2	1.8	176	22.2	2.7	+2.0	5.87	<0.001
SA/mass	73	2.94	0.15	176	2.79	0.17	−0.15	6.45	<0.001

[1] M, mean; SD, standard deviation; BMI, body mass index; SA, surface area.

Analysis

Several derived indices were also calculated from the reported means of the anthropometric dimensions above. These include: 1) the body mass index (BMI), 2) surface area/mass ratio (SA/mass) and 3) relative sitting height (RSH). The BMI was calculated as [body mass (kg)]/[stature (m)^2]. Surface area was estimated by using the equation of Gehan and George (1970), as recommended by Bailey and Briars (1996):

$$\ln SA = -3.751 + 0.422 \ln(\text{stature}) + 0.515 \ln(\text{mass}),$$

where stature is in cm, mass is in kg, and SA is in m^2. SA/mass was then determined as body SA(cm^2)/mass(kg). RSH was calculated as: [sitting height (cm)]/[stature (cm)].

Like Roberts' (1953) study, bivariate regression and correlation analyses were used to examine the relationships between mass and mean annual temperature in the current data set. Roberts' original analyses were also replicated by using the data reported in the appendix of his 1953 report after converting the temperature values from the original Fahrenheit to the Celsius scale. In addition, several new regression analyses were carried out on both the current data set and that of Roberts. These included examinations of the relationships between BMI, SA/mass, and RSH and mean annual temperature.

Both multiple regression analyses and t-tests were used to test for secular changes in body size and proportions. In the multiple regression analyses, mean annual temperature and "year of study publication" were entered as independent variables to assess temporal changes in body morphology after controlling for the influence of climate. To further assess the differences in secular trends in different climatic zones, t-tests

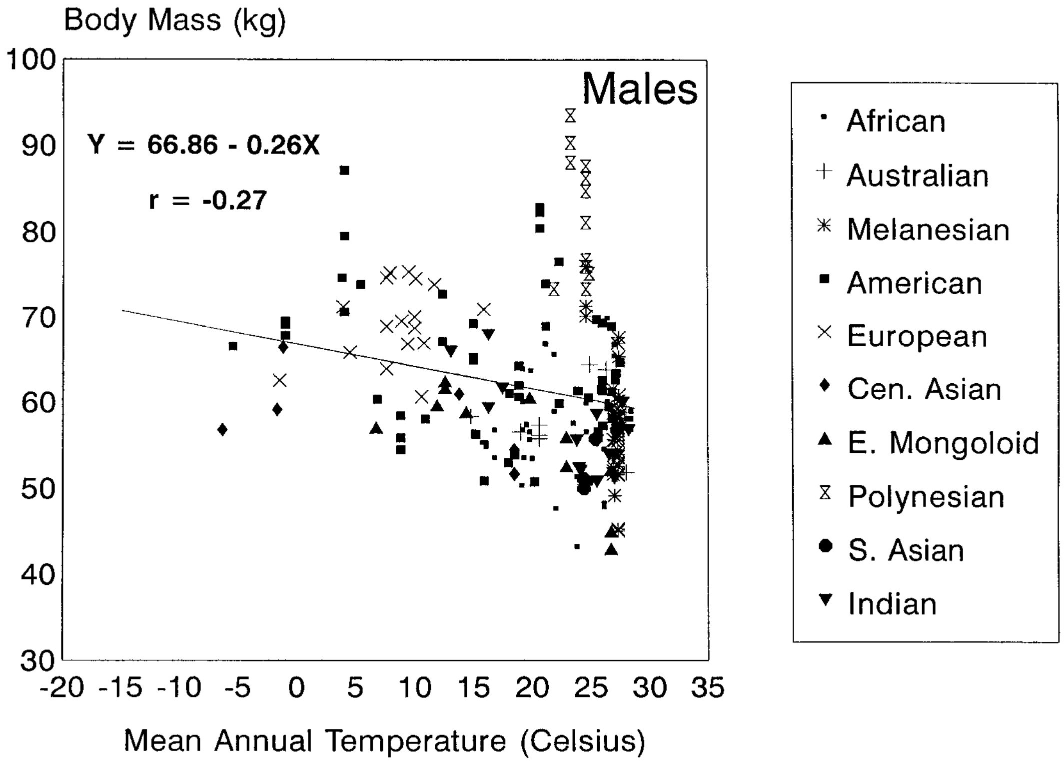

Fig. 2. Plot of body mass vs. mean annual temperature among males of the current sample.

were used to compare anthropometric measures of males in the current sample to those of Robert's sample for those populations living in cooler (mean annual temperature <15°C) and warmer (≥15°C) climates.

RESULTS

Climatic influences

Table 3 presents the results of the bivariate regression analyses for the men and women of the current sample and for Roberts' (1953) sample. In each group, body mass and the BMI are negatively correlated with mean annual temperature. In males of the present sample, the correlations between mean annual temperature and the BMI are –0.267, and –0.221, respectively, whereas the correlations for females are −0.279 for body mass and -0.295 for the BMI. For the Roberts' sample, the correlations are stronger (r = −0.589 for mass; r = −0.586 for BMI), and the slopes of the best-fit regressions are significantly steeper than in the current male sample (mass: b = −0.546 vs. −0.261, $P < 0.001$; BMI: b = −0.141 vs. −0.058, $P < 0.001$).

The SA/mass ratio is positively associated with mean annual temperature in all three samples, indicating that people inhabiting hotter regions have physiques that maximize surface area per unit body mass. However, as noted with body mass, the correlations are substantially higher in Roberts' (1953) sample (r = 0.594) than they are in the current male and female samples (males, r = 0.288; females, r = 0.341). Similarly, the regression slopes of the Roberts' sample are twice as large as those seen for in the current samples [b = 0.012 vs. 0.005 (males) and 0.006 (females); $P < 0.001$].

Finally, in the current sample, RSH is correlated negatively with temperature in both sexes (males, r = −0.369; females, r = −0.456). This relationship indicates that tropically adapted populations have a more

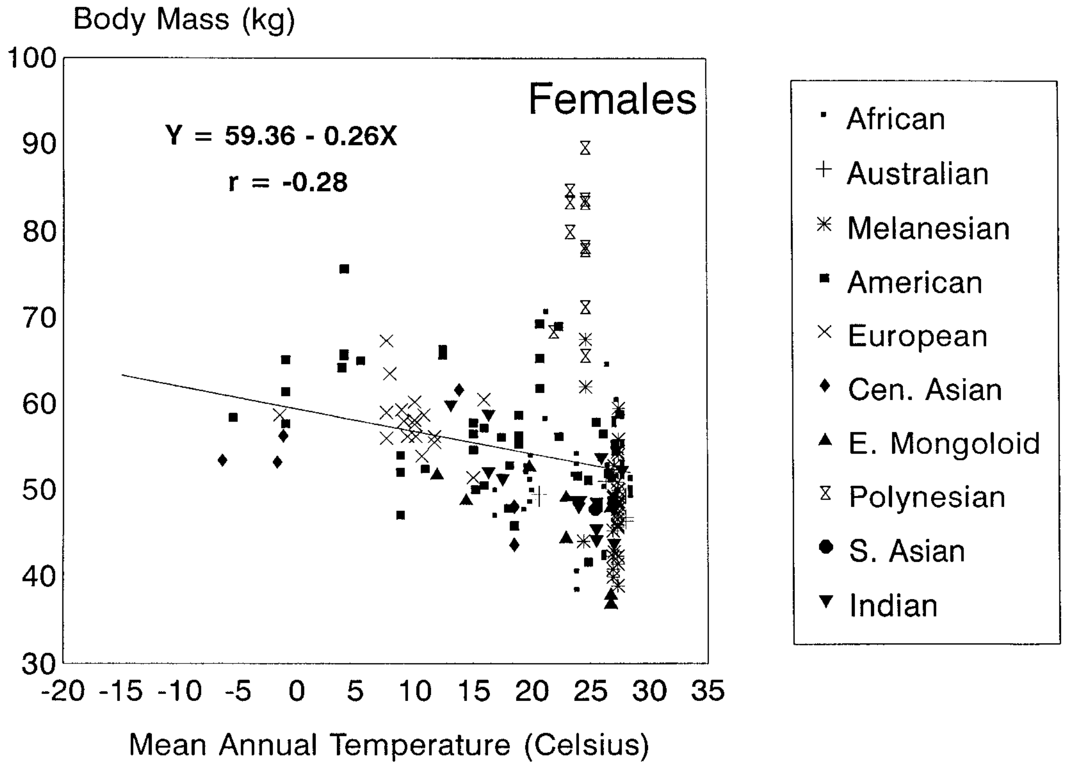

Fig. 3. Plot of body mass and mean annual temperature among females of the current sample.

linear body build that is characterized by relatively longer leg lengths. Like in the above analyses, the correlations and regression slopes obtained in the present study are more modest than those obtained by Roberts (1973; r = −0.62; b = −0.12).

Secular trends

To investigate how the impact of climate on body morphology has changed since 1953, multiple regression analyses were performed in which "year of study publication" and "temperature" were both entered as independent variables. The results presented in Table 4 indicate that there is a significant temporal influence on several of the anthropometric indices, even after the climatic effects have been accounted for. Body mass and the BMI have increased significantly over the years in one or both sexes, whereas SA/mass has declined. In contrast, modest declines in RSH are evident; however, these changes are not statistically significant in either sex. Consequently, it appears that measures of mass have changed more markedly than body proportions over the last 40 years.

The secular trends in body size, however, do not appear to be equal across populations of different climatic zones. This point is evident in Table 5, which presents differences in mass, BMI, and SA/mass between the current male sample and Roberts' (1953) sample for groups living at mean annual temperatures <15°C and those living in areas ≥15°C. It appears that increases in body mass are greater among populations of warmer climates. For populations living in warmer areas, there is a 6.9 kg difference in mass between Robert's sample and the present sample, compared with only a 4.7 kg difference in the cooler regions. Similarly, differences in BMI between the two samples are twice as great in the warmer climates as

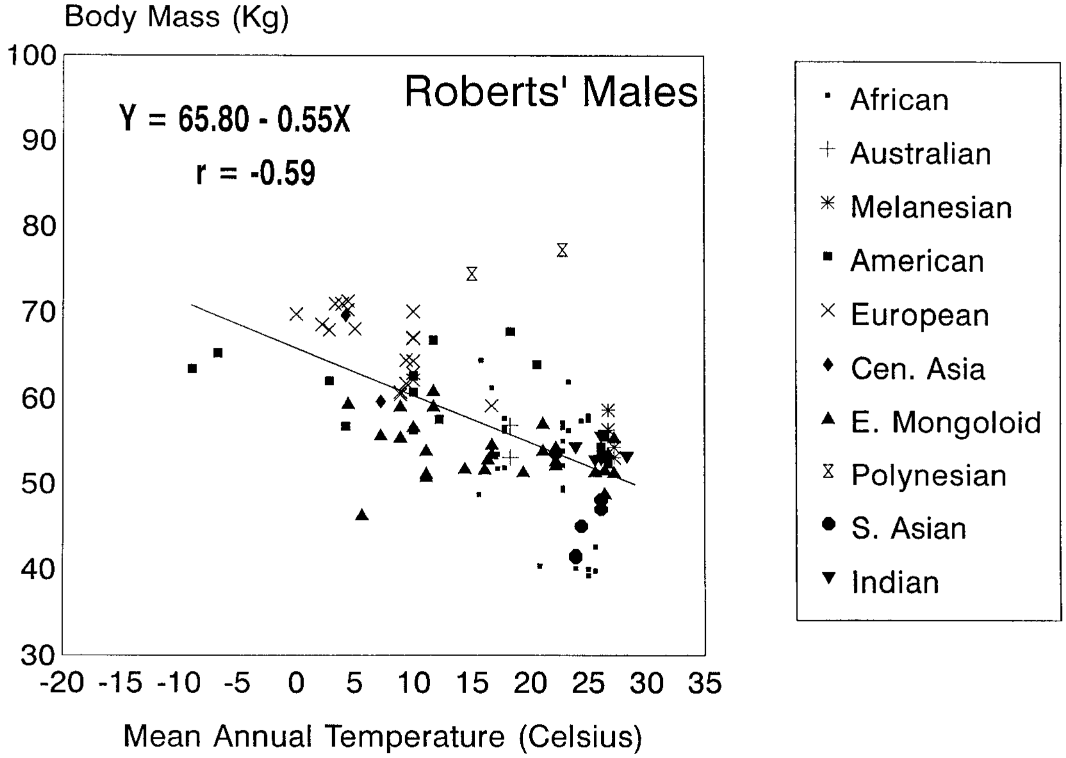

Fig. 4. Plot of body mass vs. mean annual temperature among males of the Roberts (1953) sample.

they are in the colder ones. Conversely, SA/mass ratios show sharper declines at warmer temperatures. Thus, although there has been a general, world-wide increase in body mass over the last 40 years, the increases appear to be disproportionately larger in tropical regions.

The differential increases in body mass among tropical populations are clearly evident in Figures 2–4, which present the plots of mass vs. temperature for the current sample and Roberts' sample. Figures 2 and 3 show that, in both men and women of the current sample, the greatest variation in mass occurs among tropical populations. Moreover, this variation is considerably greater than that observed by Roberts (1953; see Fig. 4). Consequently, the lower correlations and shallower regression slopes of the relationship between mass and temperature in the current analyses reflect marked increases in average size and variation among tropical populations since the 1950s.

Similar patterns are seen in Figures 5–7, which show the relationships between SA/mass and temperature for the three samples (i.e., current males, current females, and Roberts' males). Again, it is the increased variation among populations of warmer climes that explains the more modest correlations and slopes of the relationships.

Figures 8 and 9 present plots of RSH vs. temperature for the males and females, respectively, of the current sample. Like the body mass measures, the greatest variability in this index is seen among tropical populations. Specifically, the Australian aboriginal populations typically display very linear body builds (i.e., low relative sitting heights), whereas Melanesian groups show RSHs that are more similar to those of northern populations. Consequently, although the multiple regression analyses failed to demonstrate a

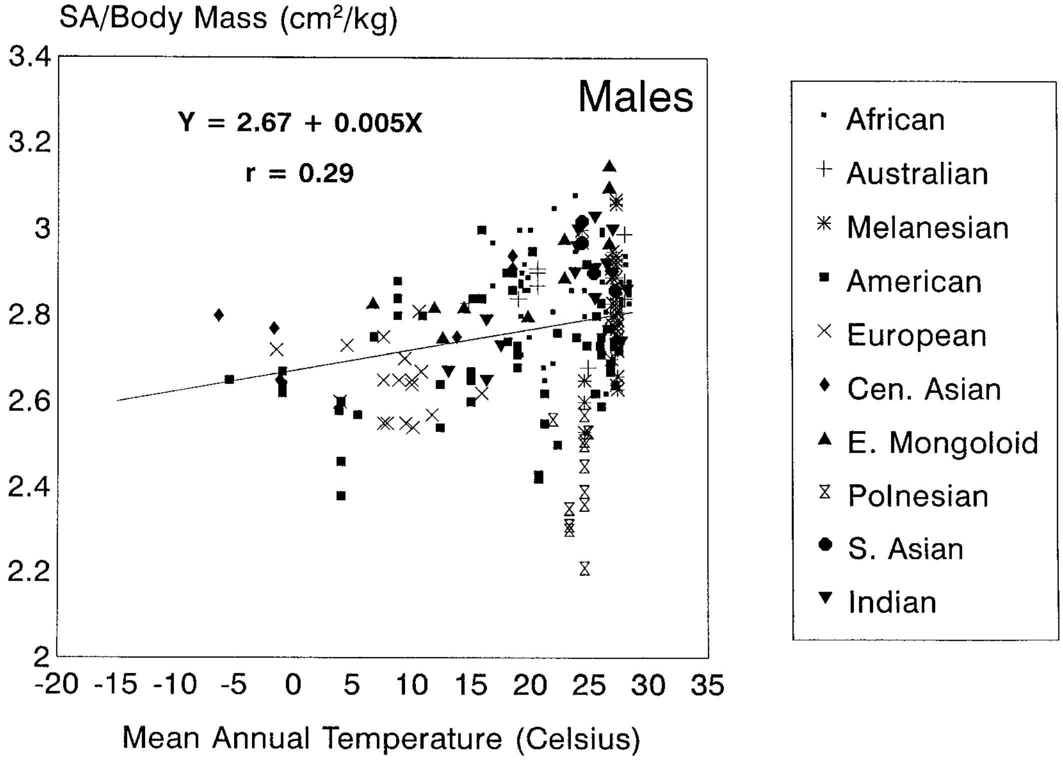

Fig. 5. Plot of surface area (SA)/mass vs. mean annual temperature among males of the current sample.

significant secular trend in body proportions, the relationship between RSH and temperature in the current sample does appear to be different than that reported by Roberts (1973; i.e., r = −0.37 for men vs. r = −0.62 in Roberts sample; r = −0.46 for women vs. r = −0.65 for Roberts' sample).

DISCUSSION

Climate and body mass

The present study largely confirms the results of Roberts (1953) in finding a significant, negative association between body weight (i.e., mass, BMI) and mean annual temperature. In addition, our results show that this relationship exists in both men and women. Roberts' (1953, 1973) previous work had been suggestive of this; however, his results were based on only a small number of female samples (n = 33).

The results are consistent with regional reports of covariation between climate and body size. Crognier (1981) reported significant negative associations between mean annual temperature and both body mass (r = −0.71) and stature (r = −0.28) in a sample of 85 male populations living in Europe and the Mediterranean. However, no indication was given about when the data had been collected. Similarly, body mass (r = −0.46) and the body mass/SA ratio (r = −0.54) were negatively associated with mean annual temperature of birth place in U.S. Army recruits (Newman and Munro, 1955). On the other hand, body mass varied directly with the temperature of the hottest month (r = 0.25) in 78 populations in sub-Saharan Africa (Hiernaux and Froment, 1976). Noting that these results are in contradiction to Bergmann's rule, the authors suggest that this ecological rule fails to apply to sub-Saharan Africans, because, in that area of the world, body size has been affected by climatic variables that are not

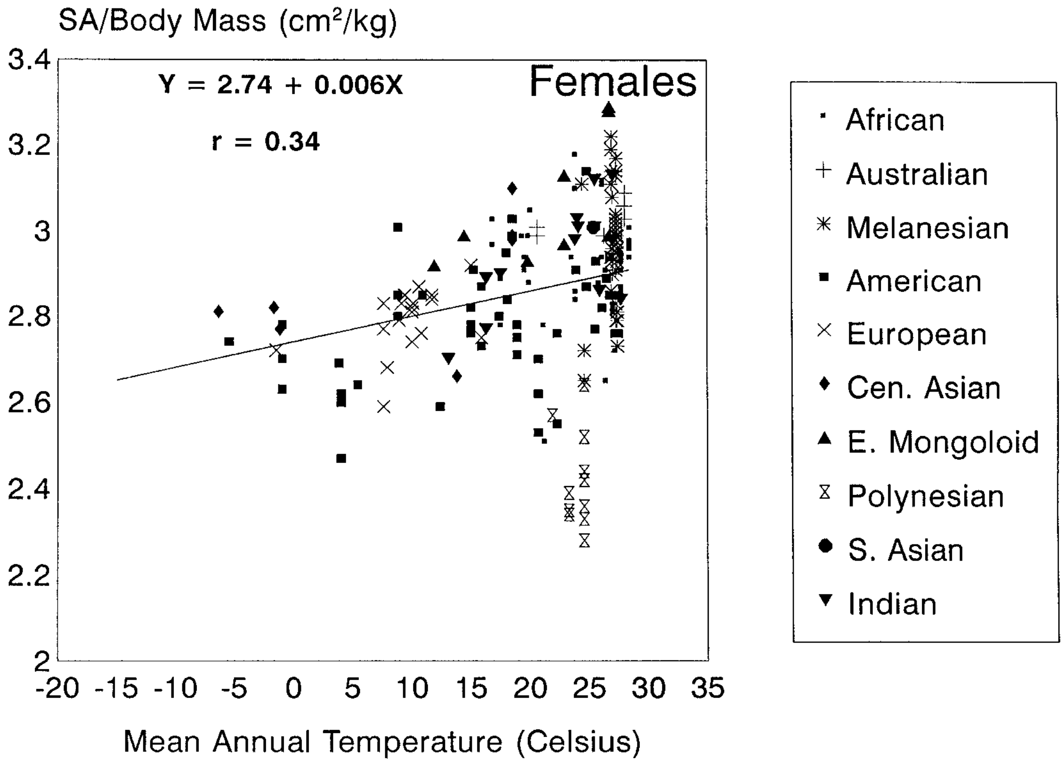

Fig. 6. Plot of SA/mass vs. mean annual temperature among females of the current sample.

captured by temperature (moisture, wind, etc.).

Some authors (see, e.g., Baker, 1958; Schreider, 1975) have questioned the use of body mass as an indicator of body size in examining the applicability of the ecological rules to humans. Schreider (1975), for example, has suggested that a ratio of body mass to SA is more appropriate, because it captures the true thermolytic characteristic of an individual. He argues that mass alone fails to convey explicitly the underlying adaptive variable (SA/body mass) and its relationship to climate. He described a gradient in which the SA/body mass ratio increases from temperate to tropical regions (Schreider, 1950), and the ratio of limbs to mass increases from temperate to tropical regions (Schreider, 1957). However, no statistical analyses were performed in this work.

Consequently, to test Schreider's hypotheses, SA/mass ratios were determined for both Roberts' original data set and the current data. There is a significant positive relationship, as predicted, between the SA/body mass ratio and mean annual temperature among both men and women of the current sample as well as Roberts' sample.

Clearly, climate plays an important role in shaping variation in body mass. However, as Roberts (1978) notes, there are many avenues through which climate may operate. Temperature, for example, may act directly as a selective agent, favoring genetic adaptations in morphology that dissipate or retain heat most efficiently. Differences in body morphology may also result from developmental responses to temperature stress. Thus, according to this developmental hypothesis, differences in adult size and proportion are acquired during growth rather than determined by genetic differences (see Frisancho, 1993). Finally, climate may shape morphology through its influence on food availability and nutrition. According to this scenario, lower body mass and linear builds

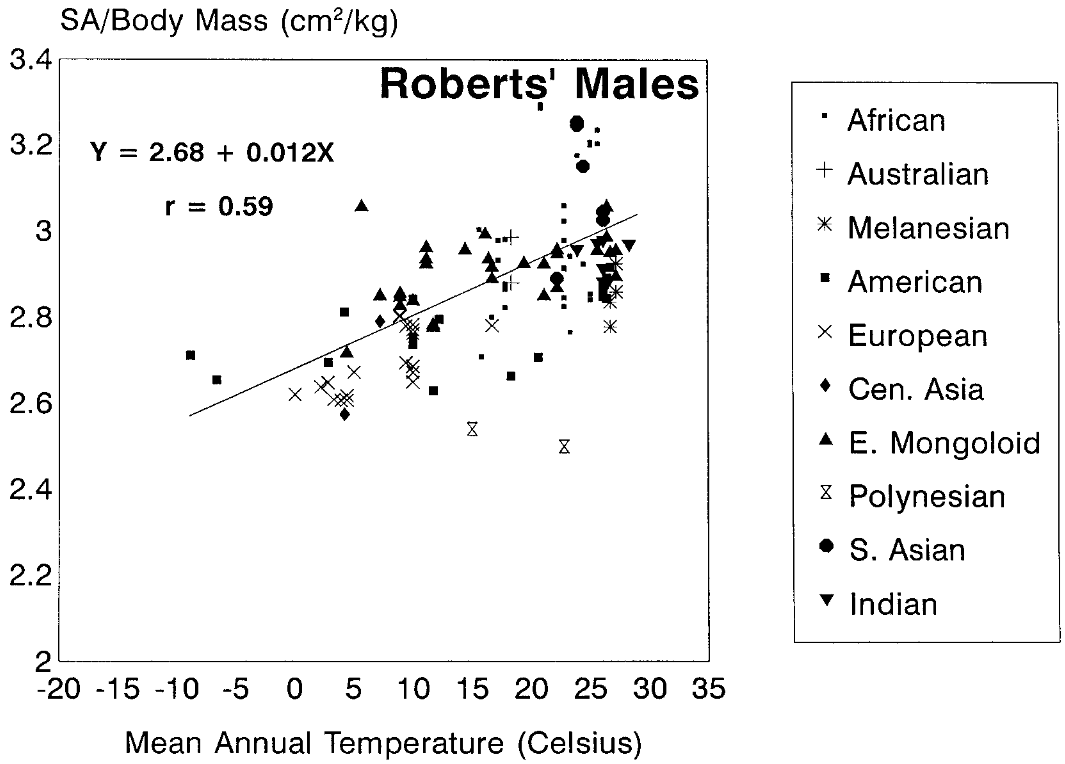

Fig. 7. Plot of SA/mass vs. mean annual temperature among males of the Roberts (1953) sample.

of tropical populations are the consequence of nutritional rather than thermal stress.

The current study and that of Roberts (1953) are limited by the use of mean annual temperature, because temperature extremes are not reflected to a large extent in the mean. Analyses aimed at the mean temperatures of the hottest and coldest months have been performed on the regional level (Newman and Munro, 1955; Hiernaux and Froment, 1976; Crognier, 1981), and further world-wide analyses using these specific stressors are warranted.

To date, most authors seem to favor the genetic/temperature explanation for the climatic variation in human body morphology, as implied by the original ecological rules of Bergmann and Allen (see, e.g., Schreider, 1964, 1975). Ruff (1994), for example, sees climatic (temperature) adaptation as a prime explanation for changes in size and proportion throughout hominid evolution. However, there is also evidence to suggest that nutrition plays a critical role. Newman and Munro (1955) demonstrated a significant association between body mass and mean annual temperature in a sample of 15,000 European American males. Because genetic constitution was held relatively constant, the authors attributed the association to regional variation in eating and activity patterns within the United States. Consequently, these results support the hypothesis that nutritional variation due to climatic differences is important in describing the association between body mass and mean annual temperature on a regional basis.

The results presented here seem to support the influence of factors other than mean annual temperature in explaining worldwide variation in body mass. Although the patterns of association in the current sample are similar to those of Roberts (1953), the current male and female samples display much lower correlations and significantly shallower regression slopes than those ob-

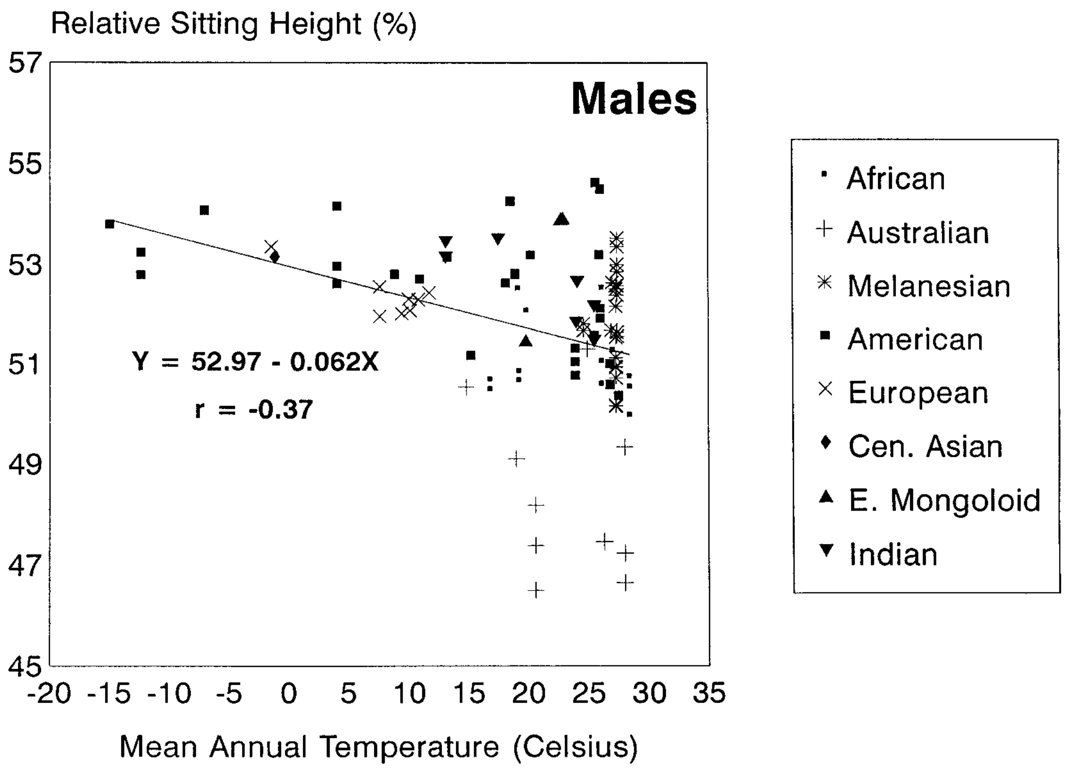

Fig. 8. Plot of relative sitting height vs. mean annual temperature among males of the current sample.

tained from the Roberts' sample. These differences are the consequence of positive secular trends in body mass over the last 40 years resulting from westernization of lifestyle and dietary patterns. These positive secular trends are most exaggerated among tropical populations (Table 5) and have been reported in Polynesians in particular (see, e.g., Baker et al., 1986; McGarvey, 1991). Increases in body mass among Polynesians are influencing the slopes of the regressions more than those among other groups. Consequently, the decline in the strength of association between body size and climate in this study suggests that the very strong, inverse relationship between mass and temperature initially reported by Roberts was attributable partly to differences in diet and nutrition as well as differences in thermal stress.

Climate and body proportions

The proportion of the body accounted for by the lower extremities appears to be associated with mean annual temperature. Although there was no evidence for a secular trend in the RSH based on the multiple regression analysis, the relationship between RSH and temperature is not the same in the present sample as it is in Roberts' (1973, 1978) sample. The slope of the best-fit regressions of the current male and female samples is only half that of Roberts' (1973) sample (males: $b = -0.06$ vs. $b = -0.12$; females: $b = -0.07$ vs. $b = -0.13$). Although some of this difference may be due to differences in the geographical composition of the samples, these results imply that there have been some changes in body proportion over the last 50 years.

The fact that the associations between RSH and climate have changed less than those between body mass and climate is not surprising, given that the heritability of body proportions is likely greater than that of body mass (Mueller, 1986). Nevertheless, the findings presented here suggest that

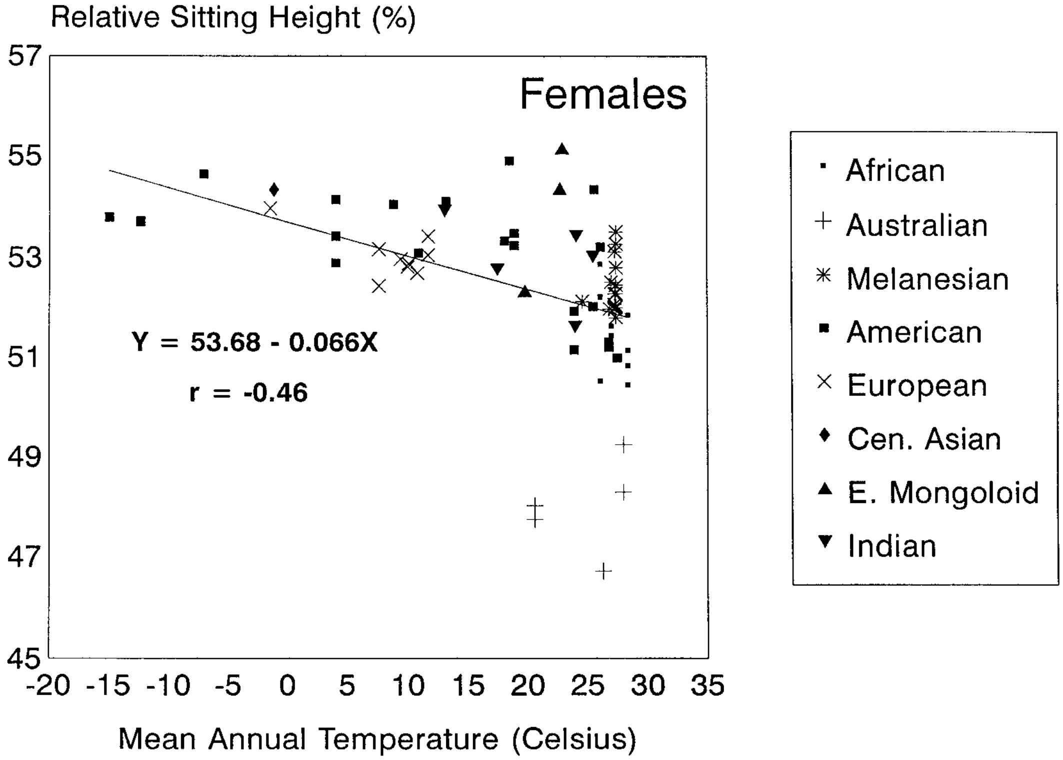

Fig. 9. Plot of relative sitting height vs. mean annual temperature among females of the current sample.

there is a significant developmental component to RSH, which is shaped by the influence of nutrition and other environmental parameters.

CONCLUSIONS

Humans appear to conform to the ecological rules of Bergmann (1847) and Allen (1877). The relationships between measures of body size and mean annual temperature are consistent with previous work of Roberts (1953). Similarly, climatic variation in body proportions is also comparable to that reported by Roberts (1973). However, despite the broad similarity in relationships, the strength of the associations has declined. The weaker correlations and more modest regression slopes are the result of marked secular trends in mass, most notably among tropical populations. This trend likely reflects the impact of acculturation and lifestyle change and the associated improvements in health care and nutrition. These improvements have disproportionately affected developing world populations of the tropics and subtropics. Thus, the strong associations between body size and temperature reported previously by Roberts and others reflect the adaptations to joint influence of thermal and nutritional stress. Over the last 50 years, these associations have become attenuated as acculturation and lifestyle changes have resulted in greater similarity in dietary adequacy and nutritional status.

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APPENDIX: List of Samples Used in the Climatic Analyses

Country/area	Population/ location	Sex	Reference
African			
Upper Volta	Dogon	M, F	Huizinga, 1977
Upper Volta	Kurumba	M, F	Huizinga, 1977
Upper Volta	Fali Ting	M, F	Huizinga, 1977
Upper Volta	Fali Kangou	M, F	Huizinga, 1977
Upper Volta	Fulani	M, F	Huizinga, 1977
Benin	Manta	M, F	Van Liere et al., 1994
Benin	Manta	F	Ategbo et al., 1995
Botswana	Bushmen	M	Wyndham, 1970
Cen. Afr. Rep.	Pygmies	M, F	Pennetti et al., 1986
Cen. Afr. Rep.	Bagandu Pygmies	M, F	Cavalli-Sforza, 1986
Cen. Afr. Rep.	Bagandu, Issongo	M, F	Cavalli-Sforza, 1986
Chad	Sara-rural	M, F	Crognier, 1969
Chad	Sara	M, F	Huizinga, 1977
Chad	Sara Majingay	M, F	Crognier and Nakroumi, 1981
Congo	Kasai	M	Hiernaux, 1964
Congo	Katanga	M	Hiernaux, 1964
Congo	Bayenga Pygmies	F	Vincent et al., 1962
Congo	Bayenga Bantu	F	Vincent et al., 1962
Egypt	Farmers	M	Wiercinski, 1970
Egypt	Professionals	M	Wiercinski, 1970
Egypt	Alexandria	M, F	Attallah, 1987
Ethiopia	Debarech	M, F	Harrison et al., 1969
Ethiopia	Adi-Arkai	M, F	Harrison et al., 1969
Kenya	Turkana	M, F	Little and Johnson, 1986
Malawi	Northern-rural	M, F	Pelletier et al., 1991
Malawi	Bantu	M, F	Burgess and Wheeler, 1970[1]
Mali	Torokoro	M, F	Dettwyler, 1992
Mali	Merediela	M, F	Dettwyler, 1992
Mali	Famabougou	M, F	Dettwyler, 1992
Mali	N'Tenkoni	F	Dettwyler, 1992
Mali	Dogo	F	Dettwyler, 1992
Mali	Siramana	F	Dettwyler, 1992
Morocco	Ben Jillali	M, F	Crognier and Nakroumi, 1981
Namibia	!Kung San	M	Winkler and Kirchengast, 1994
Nigeria	Lagos	M, F	Johnson, 1970
Nigeria	Ibadan-well off	M, F	Janes, unpublished[1]
Nigeria	Ibadan-slum	M, F	Janes, unpublished[1]
Rwanda	Tutsi	M	Hiernaux, 1965a,b
Rwanda	Hutu	M	Hiernaux, 1965b
Rwanda	Tutsi	F	Heintz, 1963
Rwanda	Hutu	F	Heintz, 1963
South Africa	Durban Zulus	M, F	Slome et al., 1960
South Africa	Venda-urban	M	Loots and Lamprecht, 1971
South Africa	Venda-rural	M	Loots and Lamprecht, 1971
South Africa	Venda-urban	M	de Villiers, 1972
South Africa	Venda-rural	M	de Villiers, 1972
Sudan	Dinka	M	Roberts and Bainbridge, 1963
Sudan	Shilluk	M	Roberts and Bainbridge, 1963
Sudan	Fur	M, F	Sukkar, 1976
Sudan	Nubians	F	Valsik et al., 1970
Tanzania	Hadza	M, F	Barnicot et al., 1972
Yemen, Democr.	Aden	F	Bagenholm et al., 1988
Yemen, Democr.	Rural	F	Bagenholm et al., 1988
Zaire	Efe pygmies	M, F	Dietz et al., 1989
Zaire	Lese	M, F	Dietz et al., 1989
Australian			
Australia	Murrayians	M	Birdsell, 1967
Australia	Aborigine	M, F	Abbie, 1967
Australia	Carpentarians	M	Birdsell, 1967
Australia	Rembarranga	M, F	Prokopek, 1977
Australia	Manigrada	M	Macho and Freedman, 1987
Australia	Kalamburu	M, F	Macho and Freedman, 1987
Australia	Yuendumu	M	Macho and Freedman, 1987
Australia	Haast's Bluff	M, F	Macho and Freedman, 1987
Australia	Yalata	M	Macho and Freedman, 1987
Australia	Beswick	M, F	Macho and Freedman, 1987
Australia	Arnem Land	M, F	Jones and White, 1994

APPENDIX: (continued)

Country/area	Population/ location	Sex	Reference
Melanesian			
Fiji	Coastal villages	M, F	Hawley and Jansen, 1971
Fiji	Lau	M	Lourie, 1972
Fiji	Melanesian	M, F	Clegg, 1989
Indonesia	Jogjakarta	M, F	Bailey, 1962
Indonesia	West Java	M, F	Bailey, 1962
New Guinea	Simbai	M, F	Champness et al., 1960
New Guinea	Wosera	M, F	Bailey, 1963
New Guinea	Kalabu	M, F	Bailey, 1963
New Guinea	Baiger	M, F	Bailey, 1963
New Guinea	Wabag	M, F	Wolstenholme and Walsh, 1967
New Guinea	Lumi	M, F	Wark and Malcolm, 1969
New Guinea	Kaiapit	M, F	Malcolm, 1969
New Guinea	Chimbu	M, F	Malcolm, 1969
New Guinea	Kukukuku	M, F	Malcolm, 1969
New Guinea	Bundi	M, F	Malcolm, 1970a
New Guinea	Asai Valley	M, F	Malcolm, 1970b
New Guinea	Megiar	M, F	Malcolm, 1971[1]
New Guinea	Okapa	M, F	Malcolm, 1971[1]
New Guinea	Manus	M, F	Heath and Carter, 1971
New Guinea	Gadsup	M	Littlewood, 1972
New Guinea	Tairora	M	Littlewood, 1972
New Guinea	Auyana	M	Littlewood, 1972
New Guinea	Awa	M	Littlewood, 1972
New Guinea	Ontenu	M	Littlewood, 1972
New Guinea	Karkar Islands	M, F	Harvey, 1973[1]
New Guinea	Lufa	M, F	Harvey, 1973[1]
New Guinea	Kaul	M, F	Norgan et al., 1974
New Guinea	Lufa	M, F	Norgan et al., 1974
New Guinea	Kaul	M, F	Norgan, 1995
New Guinea	Lufa	M, F	Norgan, 1995
New Guinea	Wopkaimin	M, F	Lourie et al., 1986
New Guinea	Bundi	M, F	Zemel and Jenkins, unpublished[2]
New Guinea	Manus-pere	M, F	Schall, unpublished[2]
New Guinea	Manus-town	M, F	Schall, unpublished[2]
New Guinea	Ningerum	M, F	Hyndman et al., 1989
New Guinea	Awin	M, F	Hyndman et al., 1989
New Guinea	Yonggom	M, F	Hyndman et al., 1989
New Guinea	Gidra	M, F	Hyndman et al., 1989
Sarawak	Iban	M, F	Strickland and Ulijazek, 1993
Solomon Islands	Aita	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Nagovisi	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Nasioi	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Baegu	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Kwaio	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Lau	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Ulawa	M, F	Friedlaender and Rhodes, 1987
Solomon Islands	Ontong Java	M, F	Friedlaender and Rhodes, 1987
American			
Amazonia	Tukano	M, F	Milton, 1983
Amazonia	Maku	M, F	Milton, 1983
Bolivia	Aymara	M, F	Mueller et al., 1980
Brazil	Caingang	M, F	Keiter and Salzano, 1963
Brazil	Cayapo	M, F	Da Rocha and Salzano, 1972
Brazil	Xavante	M, F	Niswander et al., 1967
Canada	Ahousat	M, F	Birkbeck et al., 1971
Canada	Anaham	M, F	Birkbeck et al., 1971
Canada	Igloolik	M, F	Shephard et al., 1973; Shephard, 1974
Canada	Upper Laird	M, F	Lee and Birkbeck, 1977
Canada	Ross River	M, F	Lee and Birkbeck, 1977
Canada	Ft. St. John	M, F	Lee and Birkbeck, 1977
Canada	Dogrib	M, F	Szathmary and Holt, 1983
Canada	Inuit	M, F	Rode and Shephard, 1995
Canada	First Nation	M, F	Katzmarzyk, 1997
Canada	Foxe Basin-Inuit	M, F	Auger et al., 1980
Chile	Arica	M, F	Arteaga et al., 1968
Chile	Aymara-coast	M, F	Mueller et al., 1978
Chile	Aymara-sierra	M, F	Mueller et al., 1978
Chile	Aymara-Altiplan	M, F	Mueller et al., 1978

APPENDIX: (continued)

Country/area	Population/ location	Sex	Reference
Chile	Laborers	M	Winslow et al., 1990
Colombia	Cali	F	Dufour et al., 1994
Cuba	Havana	M, F	Laska-Mierzejewska, 1967
Ecuador	Chachi	M, F	Stinson, unpublished[2]
Guatemala	Maya	M	Mendez and Behrhorst, 1963
Guatemala	Maya	F	Sabharwal et al., 1966
Guatemala	Highlands	M, F	Immink et al., 1992
Guatemala	Highlands	M, F	Diaz et al., 1991
Jamaica	Urban	M, F	Ashcroft et al., 1966
Jamaica	Rural	M, F	Ashcroft et al., 1966
Mexico	Trigue	M	Comas and Faulhaber, 1965
Mexico	Saltillo	M, F	Lees and Crawford, 1976
Mexico	Tlaxcala	M, F	Lees and Crawford, 1976
Mexico	Oaxaca	M, F	Malina et al., 1983b
Nicaragua	Miskito	M	De Stefano and Jenkins, 1972
Nicaragua	Sumo	M	De Stefano and Jenkins, 1972
Nicaragua	Subtiava	M	De Stefano and Jenkins, 1972
Nicaragua	Ladinos	M	De Stefano and Jenkins, 1972
Nicaragua	Rama	M	De Stefano and Jenkins, 1972
Peru	Quechua	M, F	Frisancho and Baker, 1970
Peru	Cashinahua	M, F	Johnston et al., 1971
Peru	Quechua-high	M, F	Frisancho et al., 1975
Peru	Quechua-low	M, F	Frisancho et al., 1975
Peru	Shipibo	F	Hanna and Baker, 1974
Surinam	Bushnegroes	M, F	Luyken and Luyken-Koning, 1961
Surinam	Wajana	M, F	Glanville and Geerdink, 1970
Surinam	Trio	M, F	Glanville and Geerdink, 1970
United States	Apache	M	Kraus, 1961
United States	Fort Belknap	M, F	ICNND, 1964b
United States	Blackfeet	M, F	ICNND, 1964a
United States	Seminole	M, F	Pollitzer et al., 1970
United States	Western Apache	M	Miller, 1970
United States	Wainwright	M, F	Jamison and Zegura, 1970
United States	Eskimo	M, F	Auger et al., 1980
United States	Mex-Am Barrio	M, F	Malina et al., 1983a
United States	Mex-Am Trans	M, F	Malina et al., 1983a
United States	Mex-Am Suburb	M, F	Malina et al., 1983a
West Indies	Windward Island	M	Luyken and Luyken-Koning, 1959
European			
Belgium	Brussels-students	M, F	Twiesselmann, 1969[1]
Bulgaria	National	M, F	Yanev et al., 1965[1]
Bulgaria	Sofia	M, F	Yanev et al., 1965[1]
Czechoslovakia	Czechs	M, F	Fetter and Hajnis, 1962
Denmark	National	M, F	Prokopec, 1972[1]
Finland	Helsinki-conscripts	M	Backstrom-Jarvinen, 1964
Finland	Lapps	M, F	Auger et al., 1980
France	National	F	de Felice, 1958
France	Paris-students	M, F	Kherumian and Schreider, 1967
German Dem. Rep.	Leipzig-students	M, F	Beckert, 1967[1]
Hungary	Railway workers	M	Eiben and Tari, 1970[1]
Hungary	Students	F	Eiben, 1970
Italy	Naples	M, F	Tatafiore, 1970
Italy	Sassari Province	F	de Toni et al., 1966
Poland	Warsaw	M, F	Wolanski, 1962[1]
Poland	Cracow	M, F	Kopcynski, 1972a,b
Rumania	Bucarest-students	M, F	Enachescu et al., 1964[1]
Switzerland	Basel-students	F	Heimendinger, 1964
United Kingdom	British Petroleum staff	M, F	Montegriffo, 1968
United Kingdom	JCC employees	F	Joint Clothing Council, 1957[1]
United Kingdom	Port Talbot	M	Khosla and Lowe, 1968
USSR	Moscow	M	Vlastovsky, 1966
Central Asian			
Mongolia	Khalkha Mongols	M, F	Vicek, 1965
Mongolia	Moost District	M, F	Beall and Goldstein, 1992
Nepal	Laborers	M	Winslow et al., 1990
Nepal	Tamang	M, F	Panter-Brick et al., 1992
Nepal	Tamang	F	Panter-Brick, 1992
Nepal	Kathmandu Valley	F	Malville, 1991
Siberia	nGanasan	M, F	Rode and Shephard, 1995
Siberia	Evenki	M, F	Leonard et al., 1994

APPENDIX: (continued)

Country/area	Population/ location	Sex	Reference
East Mongoloid			
Bhutan	Himalayas	M, F	Ward, unpublished[1]
Formosa	Formosans	M, F	Kimura and Tsai, 1967
Japan	Tokyo-students	M, F	Nagamine and Suzuki, 1964
Japan	Military-urban	M	Miyashita and Takahashi, 1971
Japan	Military-rural	M	Miyashita and Takahashi, 1971
Japan	Ainu	M	Shephard, 1974
Luzon	Agta	M, F	Headland, 1989
Philippines	National	M, F	National Coordinating Center, 1965[1]
Philipines	Agta	M, F	Goodman et al., 1985
South Korea	National	M, F	Korea Ministry of Health, 1967[1]
Taiwan	Chinese	M, F	Chen et al., 1963
Polynesian			
American Samoa	Manu'a Islands	M, F	Bindon and Baker, 1985
American Samoa	Tutuilia	M, F	Bindon and Baker, 1985
American Samoa	Tutuila	M, F	Pelletier and Hornick, 1986
American Samoa	Rural	M, F	Pearson, 1990
American Samoa	Tutuila	M, F	McGarvey et al., 1993
Hawaii	Samoans	M, F	Bindon and Baker, 1985
Hawaii	Honolulu	M, F	Pearson, 1990
Hawaii	Samoans	M, F	Pelletier and Hornick, 1986
Samoa	Ta'u	M, F	Pelletier and Hornick, 1986
Tonga	Tongans	M	Finau et al., 1983
Western Samoa	Salamumu	M, F	Bindon & Baker, 1985
Western Samoa	Samoans	M, F	Pawson, 1986
Western Samoa	Savaii	M, F	Pearson, 1990
South Asian			
Burma	Students	M, F	Burma Medical Research Council, 1968[1]
Cambodia	Cambodians	M	Philipe, 1973[1]
South Vietnam	Military	M	White, 1964[1]
South Vietnam	Military	M	Philipe, 1973[1]
Indian			
India	Rajasthan	M, F	Biswas and Bhattacharya, 1966
India	Punjab	M, F	Biswas and Bhattacharya, 1966
India	Jammu, Kashmir	M, F	Biswas and Bhattacharya, 1966
India	Assam	M, F	Das, 1971
India	Madras	M	Singh, 1975a
India	Ooty	M	Singh, 1975a
India	Punjab	M	Singh, 1975b
India	Gujarat-parents	M, F	Kaur and Singh, 1983
India	Gujarat-offspring	M, F	Kaur and Singh, 1983
India	Punjab	F	Singh and Raja, 1980
India	Calcutta	F	Chatterjee and Saha, 1993
Iran	Village	M, F	Mahloudji, unpublished[1]
Iran	Shiraz	M, F	Ayatollahi and Carpenter, 1993
Israel	Yemenite Jews	M, F	Lourie, 1973
Israel	Kurdish Jews	M, F	Lourie, 1973
Pakistan	Lahore	M, F	Underwood et al., 1967
Saudi Arabia	Asir Province	M, F	Khalid, 1995

[1] Reported in Eveleth and Tanner, 1976.
[2] Reported in Eveleth and Tanner, 1990.

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